

5.—MARINE COPEPODA FROM WESTERN AUSTRALIA.

V.—A NEW SPECIES OF *PARAMESOCHRA*, WITH AN ACCOUNT OF A NEW HARPACTICOID FAMILY, THE REMANEIDAE, AND ITS AFFINITIES.

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Paramesochra longicaudata sp. nov.

Occurrence.—Both sexes, in considerable abundance, were washed from sand 15 to 30 centimetres below the surface, between tide marks, at Cottesloe Beach (six miles from Perth).

Female.—Length 0.30–0.33 mm. Body of usual shape, with metasome wider than urosome. Rostrum very small and fused with the head. First antenna 7-segmented, with a large sensory filament on the fourth segment; second antenna 3-segmented, the middle segment with an outer seta, exopod 1-segmented, with three lateral and two terminal setae; mandible palp biramous, the distal ramus 3-segmented, the terminal segment very small and bearing two end setae; maxillule with exopodal lobes; maxilla with three inner lobes and a segmented terminal portion; maxilliped 3-segmented, with three terminal claws. The terminal segment of the distal ramus of the mandible palp can be made out only with an immersion lens.

First legs with both rami 2-segmented and prehensile, endopod longer than exopod; second, third, and fourth legs with 3-segmented exopods and 2-segmented endopods, variously armed; fifth legs with inner expansions fused into a large plate which covers the genital area. In the specimen figured (fig. 1, female and fig. 2, *p5* female) the basal expansion was asymmetrical, but other specimens showed no asymmetry (fig. 2, *g.a.*). Caudal rami a little more than three times as long as wide and twice as long as anal segment, armed with two unequal terminal setae, the longer being shorter than the urosome, and two short outer marginal setae, the distal being spine-like and pectinate. Egg-sac single, usually with three elongate eggs, similar to that shown for *Leptopsyllus constrictus* (Nicholls, 1935, p. 384).

Male.—Length 0.30 mm. Differs from the female in having a 5-segmented urosome, a modified first antenna in which only six segments could be seen, and in the fifth and sixth legs. In all other respects the male resembles the female.

This species is closest to *P. helgolandica*, Kunz (1936, 1938) from which it differs chiefly in the structure of the end segments of the fifth legs of both sexes.

Wilson (1932) placed the genus *Emertonia* in the Canthocamptidae, and a comparison shows that it is closely related to the genera *Leptopsyllus*, *Paramesochra*, and *Remanea* which have also been included in that family. A close study shows that this family has been derived from the same stock as the Diosaccidae and that the four genera referred to here cannot remain in the Canthocamptidae since they have no affinity with the Diosaccidae. It is proposed, therefore, to establish for them a new family, the Remaneidae

(to be defined below) and it will be shown that the affinities of this group are clearly with the Tachidiidae. In order to establish this relationship it will be necessary briefly to review the latter as at present constituted.

In his work on the Crustacea of Norway (1911) Sars included nine genera in this family: *Tachidius* Lilljeborg, *Pseudotachidius* T. Scott, *Tachidiella* Sars, *Tachidiopsis* Sars, *Robertsonia* Brady, *Danielssenia* Boeck, *Psammis* Sars, *Fultonia* T. Scott, and *Argestes* Sars, but, as he pointed out (loc. cit., p. 437) the last two should more properly be included in the Cletodidae. In the Systematic List prefacing his work (pp. IX.-XIV.) this change was made. In 1921 he included also *Euterpina* Norman in this family.

Monard (1927) included in the Tachidiidae all those genera originally placed there by Sars; he retained *Jonesiella* (which Sars had regarded as synonymous with *Danielssenia*) for the single species *brucei*, and added *Thompsonula* T. Scott. At the same time he placed the Tachidiidae at the start of the Chirognath Series instead of at the end, where Sars had placed it owing to the resemblance of some of its members to the Cletodidae.

Gurney (1927) removed *Robertsonia* to the Diosaccidae and later (1932, p. 17) restated his reasons for so doing since Monard (1928) had disputed the validity of this transference. In this later work Gurney included *Fultonia* and *Argestes* in the Cletodidae and comments (p. 18) that without *Robertsonia* the family "seems a natural one, and one of the most primitive."

In the same year Wilson (1932) added two more genera, *Rathbunula* and *Echinocornus*, to the family and these are referred to by Monard (1935) in a discussion of the family. Willey (1935) added yet another genus, *Argestigens*.

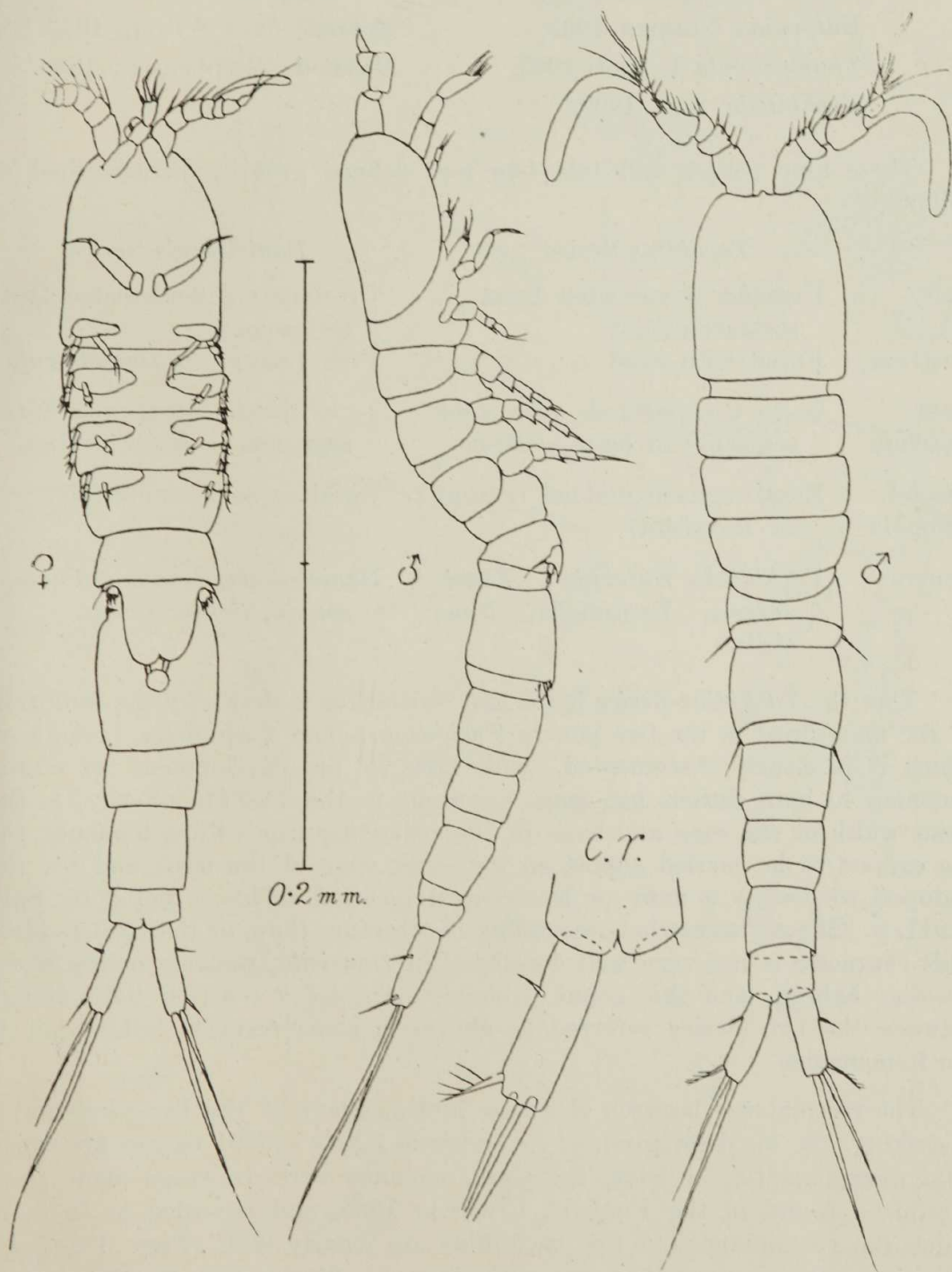
That *Robertsonia* is truly a Diosaccid has been amply demonstrated by Lang (1935) and, in his revision of the Thalestridae (1936a), he showed that *Pseudotachidius* is a Thalestrid. In his later revision of the Cletodidae (1936b) he showed that *Jonesiella brucei* belongs to *Pseudomesochra* and is thus a Diosaccid and, finally, he established the position of *Argestigens*, *Argestes*, and *Fultonia* in the Cletodidae.

Of *Rathbunula*, Monard (1935, p. 16) drew attention to its resemblance to *Thompsonula*. In Wilson's key (1932, p. 582) these genera are distinguished only by details of the fifth legs and, in fact, the second species of *Rathbunula* described by Wilson, *R. curticauda* (p. 300, Pl. 20) would, according to his key, be nearer to *Thompsonula* than to *Rathbunula*. There can be little doubt that these genera are identical and Wilson's genus, therefore, becomes a synonym of *Thompsonula*.

Here, also, we must consider *Donsiella* Stephensen (1936). This genus was placed, with some hesitation by the author, in the Laophontidae. The reasons for its removal are given in a revision of this family (Nicholls, 1941). The shape of the body, with the urosome strongly demarcated from the metasome; the broad rostrum, fused with the cephalosome; the richly setose first antenna; the 3-segmented rami of the second and third legs; the fusion between the basal segments of the fifth legs of opposite sides; the caudal rami and, in the male, the chirocerate* first antenna and modified third endopod are all Tachidiid characters, though not exclusive to this

* The terms chirocerate and subchirocerate are anglicized forms of those used and defined by Lang (1935).

family. The somewhat modified exopod in one or more of the legs of the female of *Donsiella*, and typical of many species of *Laophonte* is, however, not confined to that genus, or family, but is also found in the Tachidiidae (*Tachidius brevicornis*, in Sars, 1911, Pl. CCXIX). Against these features we have to set only the structure of the first legs. In shape these are very like those of the Laophontids, which probably caused Stephensen to include it in this family, but, unlike that of the true Laophontids, the endopod is armed with *two subequal terminal claws*. The strongly prehensile condition of these legs may be associated with the commensal habit of the species, as described by Stephensen. This condition of armature of the first endopod



Text fig. 1.—*Paramesochra longicaudata* sp. nov. Female in ventral view, male in lateral and dorsal views ($\times 340$); caudal ramus ($\times 670$).

is found also in the genus *Remanea* which, as will be shown below, is probably derived from the Tachidiidae. The caudal rami also show a striking resemblance to those of *Remanea*.

The genus *Clytemnestra* is also sometimes included in the Tachidiidae, notably by Wilson (1932, p. 292), but this genus differs in so many respects that it seems preferable to retain it in the separate family established by A. Scott (1909).

Thus the Tachidiidae is comprised of the following genera.

| | |
|-----------------------------------|------------------------------------|
| <i>Tachidius</i> Lilljeborg 1853, | <i>Psammis</i> Sars, 1909, |
| <i>Danielssenia</i> Boeck 1872, | <i>Tachidiopsis</i> Sars, 1911. |
| <i>Euterpina</i> Norman 1903, | <i>Echinocornus</i> Wilson, 1932. |
| <i>Thompsonula</i> T. Scott 1905, | <i>Donsiella</i> Stephensen, 1936. |
| <i>Tachidiella</i> Sars 1909, | |

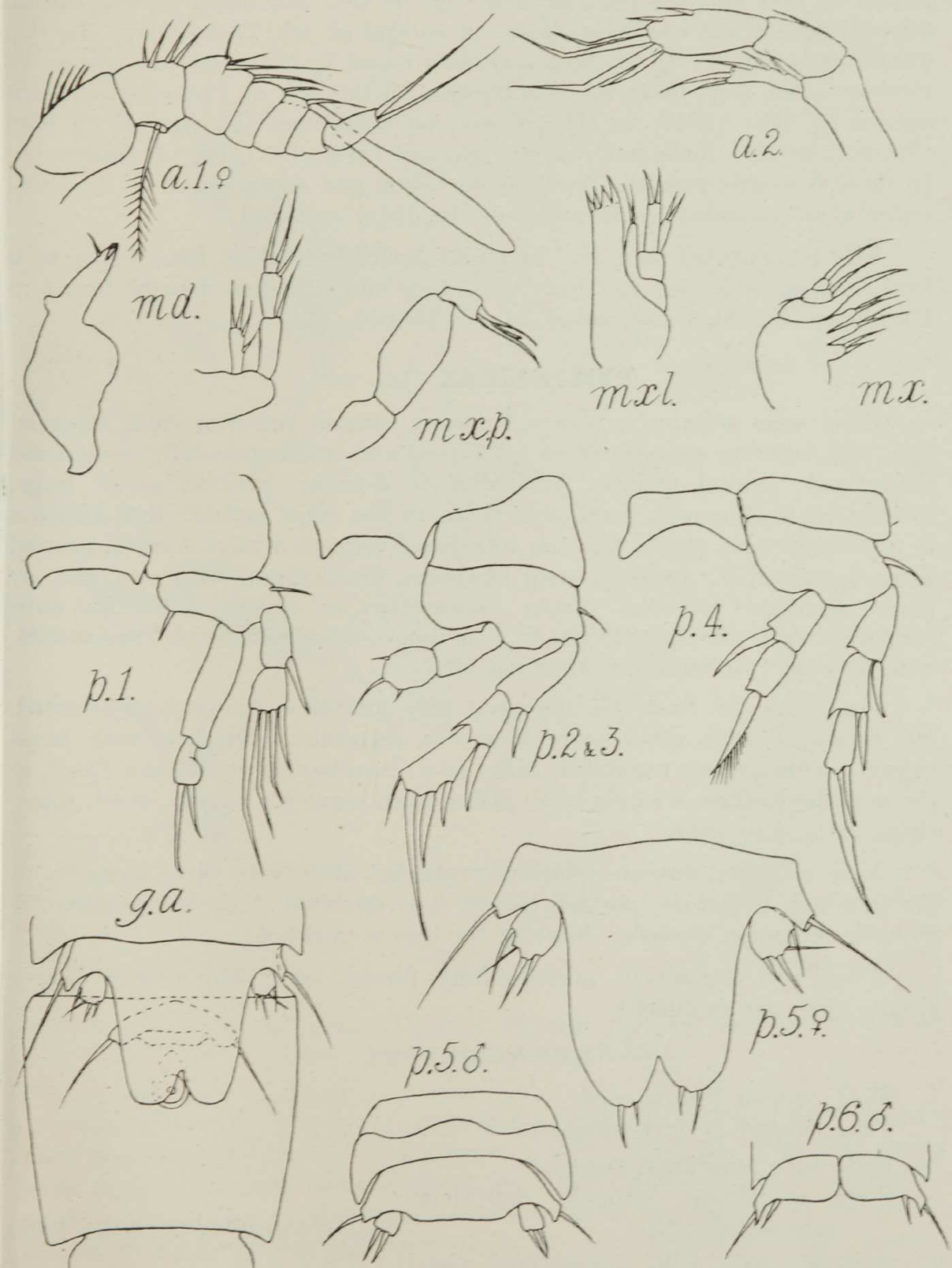
These nine genera fall into two well defined groups, distinguished as follows:—

| | <i>Tachidius</i> -Series. | <i>Danielssenia</i> -Series. |
|----------------|---|---|
| Body | Urosome demarcated from metasome | Urosome not demarcated from metasome |
| Rostrum | Fused with head | Free (except in <i>Danielssenia</i>) |
| First Antenna | 5- to 9-segmented, with four segments in basal portion | 4- to 6-segmented, with three segments in basal portion |
| Second Antenna | Basal segment divided (except in <i>Donsiella</i>) | Basal segment undivided |
| Genera | <i>Tachidius</i> , <i>Euterpina</i> , <i>Tachidiopsis</i> , <i>Tachidiella</i> , <i>Donsiella</i> . | <i>Danielssenia</i> , <i>Psammis</i> , <i>Thompsonula</i> , <i>Echinocornus</i> . |

That the *Tachidius*-Series is the more primitive is shown by the condition of the maxilliped in the two genera *Tachidiopsis* and *Tachidiella*, in both of which it is clearly 3-segmented, with little or no development of claws. Common to both Series, but more apparent in the *Tachidius*-Series, is the great width of the coxa and basis of the swimming legs with a tendency for the exopod to be carried almost on the outer edge of the basis and for the endopod to occupy a more or less central position. This is noted by Sars (1911, p. 328) as "somewhat resembling in structure those of the Cyclopoida." This character is not very well developed in *Donsiella*, possibly owing to its peculiar habitat, and this genus probably occupies a position intermediate between the two Series referred to above, in some respects linking on to the Remaneidae.

The resemblance between *Remanea* and members of the *Tachidius*-Series is striking. In his description of *R. arenicola* Klie's (1929) figures are somewhat diagrammatic. I have, therefore, included here drawings made from specimens found in the Firth of Clyde in 1935, and recorded in 1939, in which the resemblances to the Tachidiids are clearly seen (Figs. 3 and 4). These are: the shape of the body, with its wide anterior and strongly demarcated urosome; rostrum bluntly rounded; first antenna 8-segmented with four in the basal portion and well supplied with plumose setae; second antenna with

the basal segment divided, bearing a 2-segmented exopod; mandible palp biramous, the distal ramus having retained its segmented condition which is lost in *Tachidiella* and *Tachidiopsis*, although these retain the lateral setae indicating the position of fusion, and the proximal ramus 1-segmented but with lateral setae showing its recent fusion from the 4-segmented condition found in *Tachidiopsis*; maxillule with well developed exopodal lobes; maxilla with three inner lobes and no claws, the proximal lobe partly divided and the terminal portion segmented; maxilliped clearly 3-segmented, weakly



Text fig. 2.—*Paramesochra longicaudata* sp. nov. All appendages are drawn to the same scale ($\times 930$) except the genital area and male fifth and sixth legs ($\times 650$).

prehensile, with several claw-like setae. The swimming legs are of the typical Tachidiid shape and richly spinous, but the first endopod has become prehensile. The caudal rami closely resemble those of the Tachidiids and the genital area is very similar to that of *Tachidius* (cf. Lang, 1935, fig. 4) and at the same time shows a resemblance to that of *Tigriopus* (Lang, 1934, p. 9, fig. 10), a further indication of its primitive position. In the male the first antenna is subchirocerate and in the Tachidiids it is chirocerate.

This resemblance is still to be seen in *Paramesochra* (cf. Sars, 1911, Supp. Pl. 45) and the peculiar fifth legs of this and allied genera can be related only to the condition found in several of the *Tachidiidae*. In this connection compare the various conditions found in the numerous species of *Paramesochra*, *Emertonia*, and *Leptopsyllus* with those of *Tachidius littoralis* figured by Klie (1913, fig. 18), *Euterpina acutifrons* also figured by Klie (loc. cit., fig. 32), *Tachidius reductus* Monard (1935, Pl. I, fig. 11) and so on. In these is clearly seen the tendency to fusion and enlargement of the basal segment accompanied by reduction of the distal segments.

The Remaneidae then are Tachidiid derivatives which have taken to a sand-dwelling existence and have undergone the reduction usually found in Harpacticoids which have taken to this habitat.

REMANEIDAE fam. nov.

Body wide anteriorly, with a tendency towards intersegmental constriction, and tapering posteriorly or cylindrical and intersegmentally constricted throughout; genital segment undivided in female; rostrum never large, articulated in *Remanea*, small and fused in the other genera; first antenna 7- to 9-segmented; second antenna with basal segment always divided, exopod 1- or 2-segmented; mandible palp biramous, distal ramus with one, two, or three segments, proximal ramus 1-segmented or absent; maxillule with exopodal lobes; maxilla with one to four inner lobes; maxilliped 3-segmented, with at least two, subequal, terminal claws.

Legs with the basal portion very wide and rami variously segmented, but endopods with never more than two segments; fifth legs with basal segment more or less expanded, often to a considerable extent and fused in the mid-line to form a single large plate, distal segments usually small, sometimes reduced to setae.

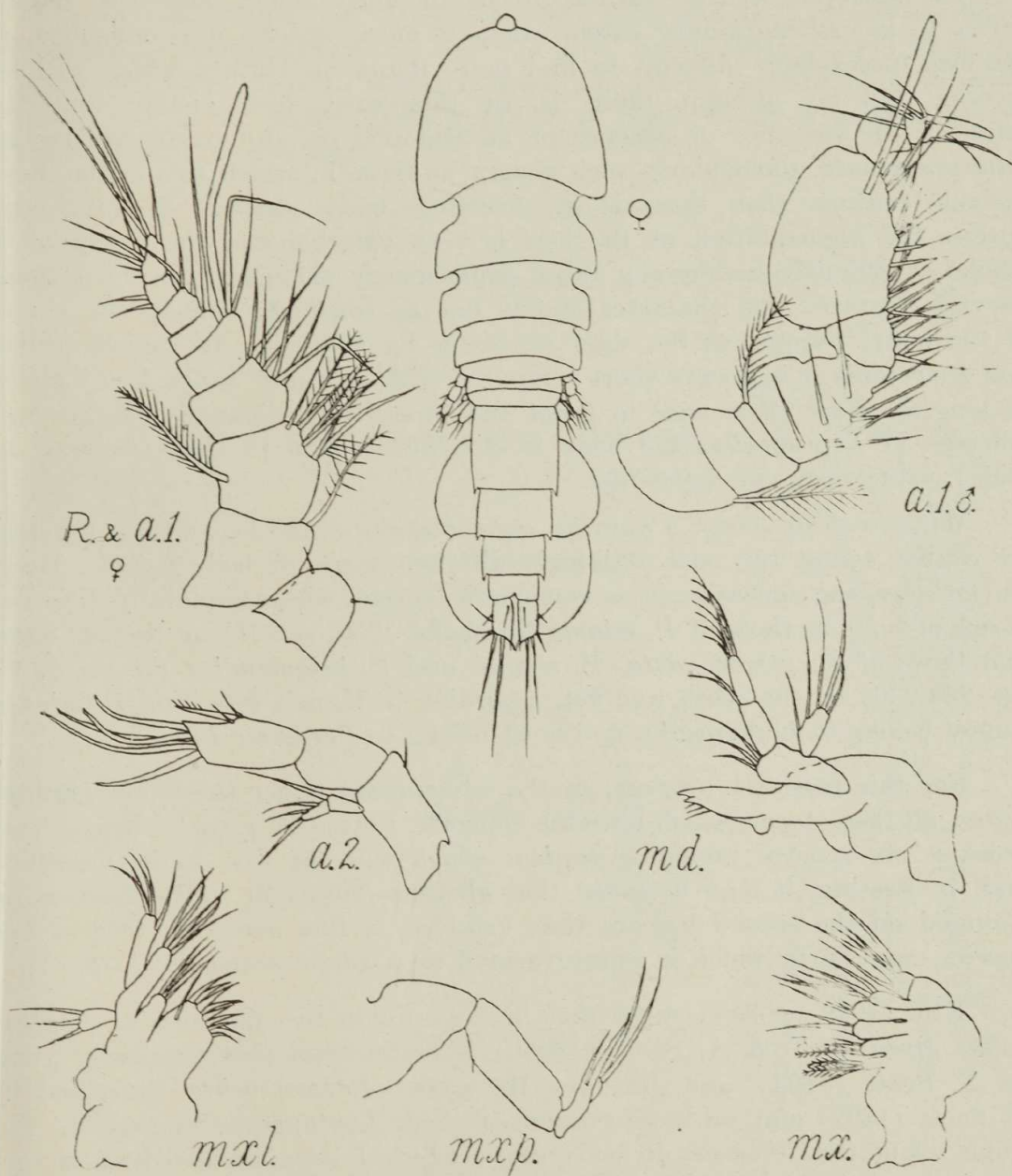
Male with first antenna subchirocerate, but often with three segments in the terminal, prehensile portion though it is doubtful if these segments are movable one upon another. None of the legs is modified.

These are exclusively sand-dwelling forms, never attaining a length greater than one millimetre.

KEY TO GENERA.

- | | |
|---|------------------------------------|
| 1. First exopod 3-segmented | <i>Remanea</i> Klie 1929. |
| First exopod 2- or 1-segmented | 2 |
| 2. Body wide anteriorly, tapering | 3 |
| Body cylindrical, strongly constricted intersegmentally | <i>Leptopsyllus</i> T. Scott 1894. |
| 3. Mandible palp with 3-segmented distal ramus | <i>Paramesochra</i> T. Scott 1892. |
| Mandible palp with 2- or 1-segmented distal ramus | <i>Emertonia</i> Wilson 1932. |

The members of this family are not very clearly defined from one another. There is little doubt that *Remanea* is the least reduced form and that *Paramesochra*, *Emertonia*, and *Leptopsyllus* are direct derivatives of *Remanea* in that order. It is in *Remanea*, therefore, that the affinities of the family will be most clearly shown and its relation to the Tachidiidae has already been demonstrated.



Text fig. 3.—*Remanea arenicola* Klie. Female ($\times 170$); appendages are all drawn to the same scale ($\times 540$).

There have been several attempts to clear up the confusion existing between *Paramesochra* and *Leptopsyllus*. Klie (1929, pp. 353, 358) united them under the older name *Leptopsyllus*, but suggested that a separation might be established on the presence or absence of an endopod on the second leg, together with certain differences in the caudal rami and fifth legs. Monard (1935, p. 61) separated them by defining *Leptopsyllus* as having a strongly elongated body and the endopods of the swimming legs lacking or reduced to one or two segments.

Kunz (1938, p. 228) in reviewing these attempts adopted the first character suggested by Klie and separated the two genera on the presence or absence of an endopod on the second leg. He discarded Monard's suggestion because both characters do not always occur together. But the same criticism applies to Klie's arrangement and Kunz himself selected only one of the characters suggested by Klie to distinguish the two genera.

The structure of the various forms included under these two names varies to an extraordinary extent and, as more species are described, it becomes increasingly difficult to find more than one feature which will be binding. In my opinion there is, in this case, less justification for selecting the presence or absence of an endopod on any particular leg to separate genera, particularly such genera as these in which this is the most variable feature, than there is in selecting body shape. In all these species the segmentation of the legs is very variable and the group as a whole is obviously undergoing rapid evolutionary changes. Amongst these varying features one character stands out as constant, namely the shape of the body, selected as the chief character by Monard. In *Paramesochra* and *Emertonia* it is always short compared with its width (only 4 to 7 times as long as wide), it is wide in front and tapers very distinctly posteriorly, whereas in *Leptopsyllus* the body is elongate (about 10 times as long as wide), cylindrical, and worm-like.

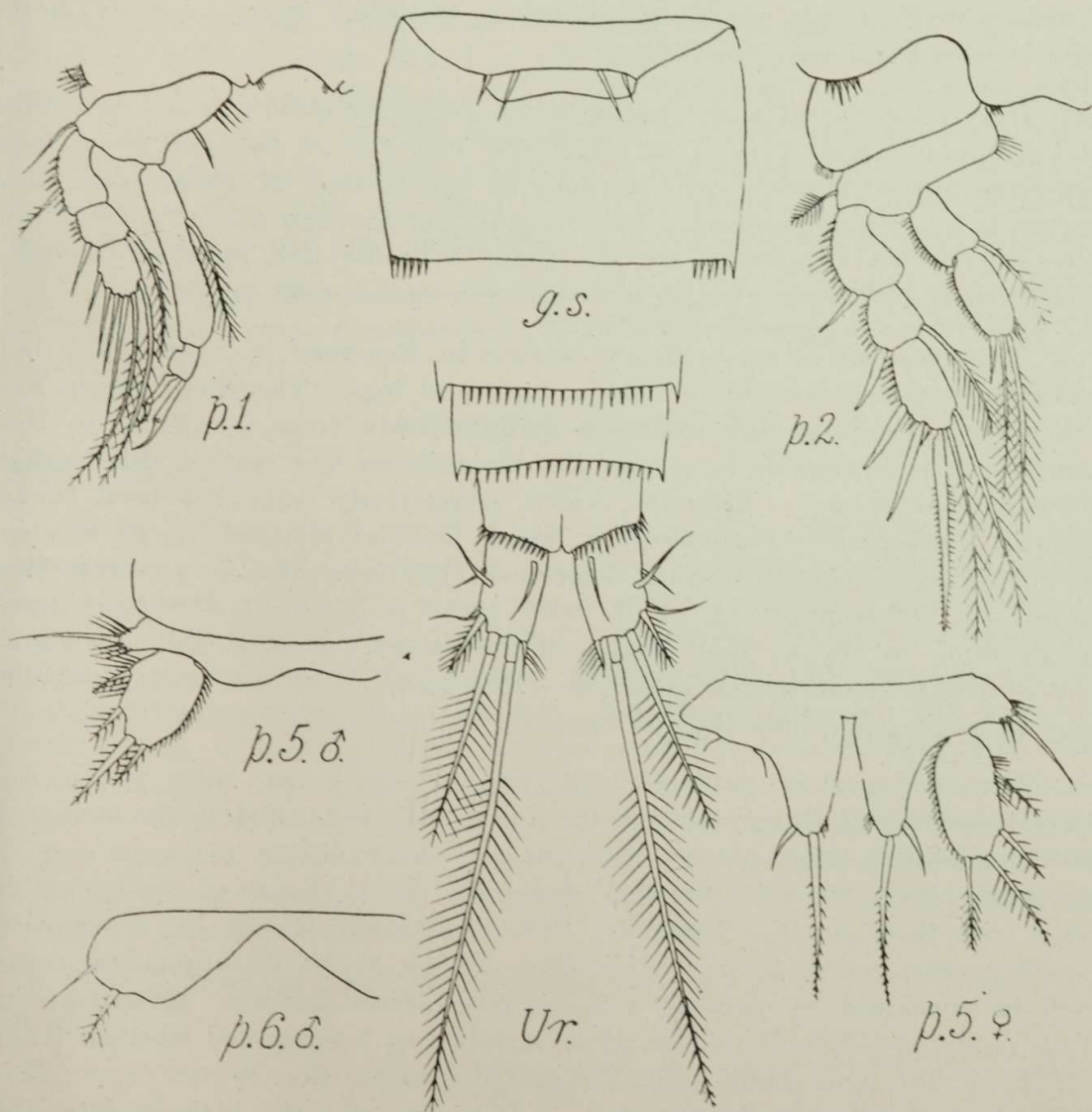
While we can accept a varying segmentation of the legs within a genus we cannot accept two such strikingly different types of body shape. How, for instance, can one reconcile as congeneric, species with such totally different forms of body as those of *P. minuta* (Nicholls, 1939, p. 337) on the one hand and those of *P. pterocaudata*, *P. similis*, and *P. helgolandica* (Kunz, 1938, pp. 233-236) on the other, and yet, according to Kunz's definition *P. minuta* cannot belong to *Leptopsyllus* and must belong to *Paramesochra*.

For this reason I propose, firstly, to separate under the name *Leptopsyllus*, all those forms which have the elongate, worm-like form of body. This removes six species, including *typicus* which was the first to be described and, in passing, it may be noted that *all* those forms in which there is no endopod on the second leg are thus included in this genus as well as one species, *minuta*, in which it is represented by a single segment.

Klie (1929, p. 353) states that in his opinion the diagnosis of *Leptopsyllus* given by T. & A. Scott (1895b) is better than that originally given by T. Scott (1894) and includes the genus *Paramesochra* described by T. Scott (1892) and, on these grounds, regards *Leptopsyllus* as invalid. The point about the difference in body shape which I have stressed here is very clearly seen in a comparison of the figures given by T. Scott when first describing these two genera. Compare the dorsal views of the females of *P. dubia* (1892, Pl. XII, fig. 18) and *L. typicus* (1894, Pl. IX, fig. 2). These differences were also noted by T. Scott in his descriptions. The diagnosis of *Paramesochra* (1892, p. 251) begins: "Body subpyriform; . . .," while that of *Leptopsyllus* (1894, p. 253) reads: "Body elongate, cylindrical, somewhat similar in form to *Cylindropsyllus* Brady." Thus T. Scott's original diagnoses stand in this respect at least.

Associated with this difference in body shape is a not unexpected difference in the shape of the egg-sac. In the wider forms the egg-sac contains two or three large, elongate eggs, two arranged side by side with the third, when present, placed transversely behind the first two and so imparting a

round shape to the sac as a whole, like that shown here for *Remanea arenicola* (fig. 3) which, however, has four eggs. This type of egg-sac is shown by T. & A. Scott (1895, Pl. V, fig. 1) for *intermedius*, by Nicholls (1935) for *constrictus* (p. 384) and for *minor* (p. 388), and where reference to the egg-sac has been made elsewhere in the literature in no case is there any indication that it is other than round. The egg-sac of *holsatica* Klie (1929, p. 356) is described as round and with few eggs; for *similis* Kunz (1938, p. 235) states that it contains two eggs, and that of *intermedius* is described as having a few large eggs (T. & A. Scott, 1895, p. 51); while that of *longicaudata* sp. nov., shows a condition similar to that of *constrictus*. In the case of *P. major* Nicholls (1939, p. 336), which is a large species, there are nine or ten eggs.



Text fig. 4.—*Remanea arenicola* Klie. Urosome ($\times 400$); other parts are all drawn to the same scale ($\times 525$).

On the other hand in *L. littoralis* Nicholls (1939, p. 328), the only species of those here regarded as belonging to *Leptosyllus*, in which the egg-sac has been described, it is elongate "with five or six spherical eggs carried one behind the other." This is the usual type of egg-sac found in those forms of Harpacticoids having elongate bodies, and is shown particularly by the psammophilous genera: *Leptastacus*, *Paraleptastacus*, *Evansula*, *Stenocaris*, etc.

The remaining species show a considerable variation in the segmentation of the endopods of legs two to four and, at first sight, might well all be included under the name *Paramesochra*. However, this group can further be divided on the structure of the mandible palp. In certain species the distal ramus of the palp is clearly 3-segmented, whereas in the remainder it has only one or two segments. Those with three segments comprise the genus *Paramesochra* while the latter group falls into Wilson's genus *Emertonia*. This is in complete conformity with the suggestion put forward by the late Dr. Wilson in a personal communication (August, 1937) in which he wrote: "Let me suggest that there are really three valid genera as follows, *Leptosyllus* with the single species *typicus*, *Paramesochra* with the species *dubia*, *intermedia*, *herdmani*, *robertsoni*, (and) *Emertonia* with the species *gracilis*, *minor*, *constrictus*, *holsatica*, *acutata*." Since he wrote, many new species have been described.

We can only assume that owing to the active evolution proceeding within this group of sand-dwellers, in which the need for an endopod grows less important in correlation with the habitat and method of progression, this ramus is undergoing reduction to be finally lost through disuse, a condition already reached in several species (both *littoralis* and *spinipes* Nicholls (1939) lack endopods on the second, third, and fourth legs).

Paramesochra is most closely related to *Remanea* in body shape but shows a certain reduction in mouth parts and legs. The whole group has taken on a sand-dwelling existence and the body form is related to this habitat. It is reasonable to assume that these forms first entered this habitat through coarse sand. *Remanea*, which is relatively wide, has been found only in coarse sand; *Paramesochra*, which includes relatively large species, is unable to inhabit fine sand; *Emertonia* has been able to penetrate fine sand by a reduction in size of the body (none over 0.5 mm.) without great modification in shape; *Leptosyllus* has acquired the same ability without loss of size by modification in shape of the body, which has become slender and worm-like, and may thus be regarded as the most successful form.

The two genera most difficult to distinguish on body shape are *Paramesochra* and *Emertonia*, but these are easily separated by the structure of the mandible palp, already referred to. In *P. dubia*, the type species, T. Scott (1892, Pl. XII, fig. 24) shows the distal ramus of the mandible palp with three distinct segments; Sars is noncommittal in his description of the species but his figure (1911, Supp. Pl. 45, *M*) of the appendage could well be construed as showing a 3-segmented distal ramus. In *intermedia* T. & A. Scott (1895, Pl. V, fig. 4) it is shown as 2-segmented whereas Kunz (1938, p. 231, and Abd. 1, fig. 5) in redescribing this species shows that this ramus is clearly 3-segmented. The two species *pterocephala* and *helgolandica* Kunz (1936 and 1938) both show a similar condition. For *herdmani* and *similis* the mouth parts have not been described but other features leave little doubt that they should be included in this genus.

In *Emertonia*, also, the mandible palp is biramous. The mouth parts were not described by Wilson (1932) but in the letter referred to above he stated that this is one of the characters by which he distinguished *Emertonia* from *Leptosyllus*, with which I had regarded it as synonymous (1935). The other characters which he enumerated in this letter as distinguishing the two genera are no longer of value owing to the addition of several new species